THE UNITED STATES NATURALIZED FLORA: LARGELY THE PRODUCT OF DELIBERATE INTRODUCTIONS[1]

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Abstract

Over the past 400 years plant immigrants have arrived in the United States in huge numbers, the results of accidental and deliberate introduction by humans. Very few immigrations, however, result in naturalizations; the environmental hazards for immigrants in a new range are usually acute and chronic. We traced the history of introduction among the naturalized taxa within a group of U.S. regions and states that span much of the environmental amplitude of the United States. Despite differences among these regions in physical environments and the length of their histories of plant immigration, the proportion of their naturalized floras that likely arrived through deliberate introductions is greater than 50 percent. Many of the first species to become naturalized in the northeastern United States were introduced as food seasonings or putative sources of medicine. Erstwhile ornamentals are prominent components of all the naturalized floras, especially in Florida. Some species introduced as sources of forage or fiber also became naturalized. Before 1900 many now naturalized species were introduced repeatedly and widely into the United States as seed contaminants through an extensive international commerce in crop seeds. The mode of entry is unknown for approximately 30 percent. The likelihood that the majority of species now naturalized in the United States has a history of deliberate introduction and post-immigration cultivation provides a plausible explanation for their persistence in a new range.

Key words: biotic invasion, environmental stochasticity, naturalization, ornamentals, seed catalogs, seed contaminants.

Comparisons of the sizes of regional naturalized floras with the total number of species that have likely arrived in these new ranges produce a commonly shared conclusion: few immigrant species ever become naturalized (sensu Mack et al., 2000). Williamson (1993) argued that this difference in the number of immigrant species, the number that reside temporarily (adventive or casual species), and the number that subsequently become naturalized differ in turn from each other by an order of magnitude. Accurate determination of these proportions is rarely possible (but see Holdgate, 1964). Nevertheless, the discrepancy between the number of species that arrive in a new range and the number that eventually persist appears huge (Williamson & Fitter, 1996). Today more than 30,000 plant taxa are commercially available in Australia (Hibbert, 1999), even more in the United States (Isaacson, 1996); most are routinely cultivated outside glasshouses or other shelter. Yet even liberal estimates put the total size of the naturalized flora for each country at less than 3000 species (Hnatiuk, 1990; Kartesz, 1994).

Pursuit of explanations for the long odds against naturalization that confront immigrant species have long attracted the attention of biologists (de Candolle, 1855; Gray, 1879) because any general explanation would aid substantially the prediction of which non-indigenous species will persist. This fascinating topic in ecology and biogeography has recently taken on added importance as nations grapple with erecting legally defensible scientific

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protocols by which they may exclude harmful non-indigenous species (Glowka & de Klemm, 1999). Despite numerous attempts to identify the few that will become naturalized among a host of immigrant species (e.g., Rejmanek & Richardson, 1996; Reichard & Hamilton, 1997), we still lack a general explanation for this numerical discrepancy, much less a predictive protocol (Williamson, 1999).

Explanation lies in a better understanding of the interaction between immigrants and the environment in a new range. All populations are subjected to multiple, random environmental events and circumstances, whether in their native or new range (Simberloff, 1988). The consequences of random detrimental events, e.g., prolonged or acute drought or frost, sudden and massive attack by predators or virulent parasites, are particularly devastating for small populations. Although the sheer size of a large population provides some numerical buffering from repeated losses of a percentage of its members, the same percent losses for a small population can rapidly bring it to extinction, unless members are replaced through reproduction or immigration, or both (Menges, 1992, 1998). Many, and perhaps most, immigrant populations are small founder populations for which there is no likelihood that individuals will be added through recurring immigration. The randomly occurring losses caused by ubiquitous environmental stochasticity can readily prove dire (Mack, 1995). Thus, even for an immigrant population with attributes that allow it to tolerate the average expression of conditions in a new environment, it could still be destroyed by the chance, repeated occurrence of extreme environmental events (Crawford, 1989; Crawley, 1989).

The *raison d'être* for cultivation is the deliberate protection of plant populations from environmental hazards, including those with stochastic expression. Such protection can allow the population to reach a numerical threshold, such that it can sustain losses arising from subsequent stochastic events. At that threshold size the population may become naturalized, even if cultivation is withdrawn. Thus, cultivation emerges as a potential counter-force to environmental stochasticity and may well facilitate naturalization (Mack, 2000).

If there is a causal link between cultivation and plant naturalization, we hypothesized that there should be a corresponding correlation between cultivation and the history of those species that have become naturalized. For example, in any naturalized flora, the majority of species should have a history that includes cultivation upon entry into the new range. Clearly, some species have no such link; immigrants could arrive in a new range and become naturalized without human dispersal or cultivation (e.g., Ridley, 1930; Mack & Lonsdale, 2001). If our hypothesis is correct, these examples would, however, form a minority of naturalizations.

To test our hypothesis we investigated the mode of pre-1900 introduction among the naturalized species within a group of continental U.S. floras and compared this evidence with similarly constructed tallies for naturalized floras from South Australia (Kloot, 1987), Hawaii (Wester, 1992), and northern Europe (Weidema, 2000). Time to naturalization can vary substantially (Mack et al., 2000). We attempted to circumvent most uncertain cases of naturalization by restricting our investigation to species that had arrived in the United States before 1900. As a result, their status as naturalized is based on at least 100 years of residence in the United States.

Methods

We recognized that our investigation could be complicated and handicapped by the sometimes conflicting synonymy of binomial names across the last two centuries and differences among floras in the definition of naturalized species. We selected published U.S. floras or checklists that identify naturalized species as those that persist without aid of recurring human cultivation; furthermore, these floras clearly make a distinction between adventive (temporary, waif, transient) species and naturalized species. Our selection criteria are met by recent floras or checklists for New York (Mitchell, 1986), Rhode Island (Gould et al., 1998), Florida (Wunderlin, 1998), and North-Central Texas (Diggs et al., 1999). We did, however, delete 46 species that Wunderlin (1998) considered naturalized because he reported that each of these species has been collected only once or has not been collected recently. We employed Fernald's (1950) *Gray's Manual of Botany*, 8th ed., because of its coverage of the northeastern quarter of the United States, a region with diverse habitats, and its frequent descriptions on the mode of introduction for non-indigenous species. These floras collectively represent much of the diversity within the continental U.S. naturalized flora.

We attempted to determine the history of introduction for each naturalized angiosperm in these floras. We deliberately excluded other plant groups from our study as the records for some of these groups (e.g., cryptogams) are much less complete and reliable. Information is rarely collected on a species' introduction event(s), although some introductions can be traced in detail (e.g., Haughton,

Table 1. Summary of the likely mode of entry (deliberate, seed contaminants, as both deliberate & seed contaminants, and unknown) for angiosperm species now naturalized in Florida, north-central Texas, the central northeastern United States, Rhode Island, and New York as derived from published floras (see footnotes 1–5). Numbers in all but the last column are the percentages of the total naturalized flora that arrived by a mode of introduction.

	Delibrate introductions	Seed contaminants	Deliberate & seed contaminants	Unknown	Number of taxa
Florida[1]	67	1	1	31	1161
North-central Texas[2]	62	2	3	34	417
Central northeastern United States[3]	59	3	3	35	559
Rhode Island[4]	59	3	3	35	408
New York[5]	57	3	4	37	391

[1] Wunderlin (1998).
[2] Diggs et al. (1999).
[3] Fernald (1950).
[4] Gould et al. (1998).
[5] Mitchell (1986).

Sources for the modes of introduction: Anon. (1882), Austin (1978), Bailey (1906), Barton (1818), Blake (1922), Coon (1974), Darlington & Wylie (1955), Darlington (1826), Darlington (1859), Darwent & Coupland (1966), de Schweinitz (1832), Diggs et al. (1999), Duke (1985), Faden (1989), Fernald (1950), Fernald & Kinsey (1943), Ferreira et al. (1997), Gordon & Thomas (1997), Grieve (1959), Haughton (1978), Hitchcock (1950), Howell (1959), Hume et al. (1983), Josselyn (1672), Lamson Scribner (1869), le Strange (1977), Long (1922), McCarthy (1888), McCartney (1984), Mack (1991), Mahler (1980), Mohr (1878), Morton (1976), Morton (1989), Muenscher (1955), Oakley & Westover (1916), Old (1981), Piper (1915), Pursh (1814), Rhoads & Klein (1993), Ridley (1930), Schery (1965), Schmitz et al. (1991), Smith (1900), Spencer (1984), Stillé & Maisch (1880), Sturtevant (1919), Tanaka (1976), Uphof (1968), Weldon et al. (1969), Wunderlin (1998).

1978; Mack, 1991; Schmitz et al., 1991, and references therein). In the absence of contemporaneous records of a species' introduction, we established criteria for identifying the most plausible introduction scenario. Species considered here to have arrived through deliberate introduction have a history of pre-1900 human use within the species' native range or in the United States. We reasoned that if a species had been used for centuries as, for example, a seasoning or herbal in western Europe (Sturtevant, 1919; Grieve, 1959), it was likely introduced deliberately by human immigrants to the United States (e.g., *Nepeta cataria* L., *Dipsacus fullonum* L., *Taraxacum officinale* Weber).

Crop seeds have been imported to North America by Europeans for more than 400 years (Viola & Margolis, 1991). Throughout most of this time seed cleaning has been either not practiced, ineffective, or even subverted (see Discussion); consequently, arriving as a seed contaminant became a likely accidental mode of entry for some species. Species were considered to have arrived by this mode if they had a pre-1850 history as seed contaminants in Europe or the United States (e.g., de Schweinitz, 1832).

For many species a pre-1900 record of use is recorded in herbals and horticultural compendia (e.g., Bailey, 1906; Fernald & Kinsey, 1943; Grieve, 1959; Uphof, 1968), plant *materia medicas* (Stillé & Maisch, 1880), pre-1860 U.S. floras (e.g., Pursh, 1814; Darlington, 1859), and 19th century state and federal agricultural publications (see footnotes in Table 1). In addition to the primary literature, we searched 19th century seed catalogs that had been distributed in the eastern United States (Mack, 1991, and references therein). These catalogs not only report a large array of non-indigenous species for sale, but most also state each species' binomial name and uses (Appendix I). Fernald (1950), Wunderlin (1998), and Diggs et al. (1999) indicated a mode of introduction for some species, and their determinations supplemented our other sources.

We initially searched in the pre-1900 literature for species under their currently accepted names. Fortunately, many plant species names have been retained since their initial description [e.g., *Rumex crispus* L., *Stellaria media* (L.) Vill.], although we usually cannot verify the species' identification in a historic account. Some naturalized species in the modern floras were left without an assigned mode of introduction because we could not reliably identify them in the 19th century literature. These were placed in the Unknown Category. The state or regional floras from which we prepared our tallies all include some naturalized subspecies and varieties. We usually could not identify these taxa within the pre-1900 botanical literature, and unidentified taxa

were also assigned to the Unknown Category. The International Plant Names Index (http://www.ipni.org) was employed as the nomenclatural standard for plant names and authorities.

Results

Results of our investigation of the history of introduction among these naturalized floras are summarized in Table 1. (Only this summary is provided here. Information on the mode of introduction for each investigated species is available from the authors upon request.) The majority of angiosperm species within each naturalized flora has a pre-1900 history of use in their native range or the United States, or both. The percentage of such deliberate use is similar among the floras: lowest within the New York flora (57%), highest in the Florida flora (67%). Some species have both a history of use and were 19th century seed contaminants (e.g., *Agrostemma githago* L., *Bromus secalinus* L., *Centaurea cyanus* L., *Convolvulus arvensis* L., *Ranunculus acris* L.) (de Schweinitz, 1832; Fernald, 1950; Grieve, 1959; Haughton, 1978; Mack, 1991). These species, which form 1 to 4% of the naturalized angiosperm floras, are recorded in Table 1 as both intentional and accidental introductions. The total percentage of these naturalized floras with a post-immigration link to cultivation, introduced either deliberately or as contaminants in crop seeds, is between 64 and 69%. The modes or circumstances under which the remainder (31–37%) arrived in their new U.S. range are unknown.

Similarity in the percentages among the floras surveyed for the central northeast United States (Fernald, 1950), Rhode Island (Gould et al., 1998), and New York (Mitchell, 1986) is due in part to the similarity of these three species lists. Differences do occur, however, and may reflect the 40- to 50-year differences in the collection spans between Fernald (1950) and the other two accounts, as well as differences in the intensity of collection. Florida's climate and less intense pattern of human settlement until the 20th century (Gannon, 1996) has yielded a naturalized flora that is largely not represented elsewhere in the conterminous United States. Most of its naturalized species have subtropical or tropical native ranges (Wunderlin, 1998), and many of these species were imported for potential use as ornamentals and maintained in government test gardens (Gordon & Thomas, 1997). This intensity of plant introduction for ornamental horticulture perhaps explains the high percentage (69%) of its naturalized flora that has a post-introduction link to cultivation.

Discussion

Our results reveal a strong correspondence between naturalized species and these species' deliberate introduction and cultivation (Table 1). Other species that arrived as seed contaminants in crop seeds would have been the collateral beneficiaries of cultivation. Together, the proportions in these two categories support the contention that cultivation, whether deliberately or inadvertently supplied for an immigrant species, could have contributed to the persistence of at least 60 percent of the naturalized angiosperm species in the regions we assessed.

The Fate of Deliberately Introduced Species

The major agent for spreading plants into new ranges around the globe for at least the past 400 years has been human immigration. In embarking on an oceanic voyage of colonization, all peoples, whether Polynesians and Melanesians across the Pacific (Whistler, 1991) or Europeans worldwide (Mack, 1999, 2001), have carefully ensured that they carry their domesticated plants with them. This motivation springs from a deep-seated need to anticipate and resolve the dilemma caused by unknown, uncertain, or at least not assured sources of food, fiber, forage, and other essential plant products in a new range. Even if would-be colonists had advance knowledge that indigenous species in their new homeland could sustain them, plans for transoceanic colonization have carefully included the transport of the germplasm of essential crops in the initial voyage. Invariably, this transfer of species that were deemed desirable, if not essential, has been maintained long after the colony's survival was assured (Mack, 1999, 2001).

The rapidity with which the early colonists in eastern North America established European crops is remarkable; dire necessity is indeed a powerful stimulus. Tuckerman (see Josselyn, 1672) cited an account by Higginson in 1629 in which he raved about the vigor and diversity of the European crops already available in New England, including beets, carrots, cabbage, asparagus, radishes, and lettuce. From the standpoint of species that were to become members of the naturalized flora, Higginson's list of introduced herbs is revealing: sorrel, parsley, chervil, and marigold for pot-herbs, along with sage, thyme, clary, anise, fennel, coriander, spearmint, and pennyroyal as "sweet herbs."

Cultivated fields and gardens with these European species produced some of the earliest naturalized species in North America. By 1672 Josselyn reported seeing "Dandelion" (*Taraxacum officinale* Weber), "Wormwood" (*Artemisia absinthium* L.),

and "Black henbane" (*Hyoscyamus niger* L.) growing outside cultivation in New England. A century later, Kalm (1770) found other species, including *Tanacetum vulgare* L. and "Datura" (*Datura stramonium* L.), that had also escaped cultivation.

The diversity of species used for medicinal purposes and as seasonings (Grieve, 1959) likely provided the largest single array of species naturalized in the United States by ca. 1800. Of the 559 species listed by Fernald (1950) as naturalized, at least 65 were in use before 1900 as herbal remedies or seasonings. Early 19th century seed catalogs often contained sections devoted to "pot-herbs" and medicinal species: many of the species in these lists are now naturalized throughout the United States (Mack, 1991). As suggested in Josselyn's (1672) list, it is likely that many of these species had been introduced much earlier. By the early 19th century some were already being listed as naturalized in regional floras, such as *Anthemis cotula* L., *Cynoglossum officinale* L., *Inula helenium* L., *Nepeta cataria* L., *Solanum nigrum* L., *Solidago odora* Ait., and *Urtica dioica* L. (Barton, 1818). In addition, Pursh (1814) noted the persistence of *Cannabis sativa* L. ("*Cannabis sativa*"), *Cichorium intybus* L. ("*Cichorium intybus*"), *Conium maculatum* L. ("*Conium maculatum*"), *Hypericum perforatum* L. ("*Hypericum perforatum*"), *Linum usitatissimum* L. ("*Linum usitatissimum*"), *Marrubium vulgare* L. ("*Marrubium vulgare*"), and *Ricinus communis* L. ("*Ricinus communis*"). Forage grasses, an early perceived deficiency within the native flora, were also actively imported (Cronon, 1983). As a result, western European pasture species were members of the pre-1800 naturalized flora: *Aira praecox* L., *Holcus lanatus* L., *Lolium perenne* L., *Phleum pratense* L., *Poa compressa* L., *Poa annua* L., *Poa pratensis* L. (Barton, 1818).

European fruit trees were planted very early in the settlement of New England (Young, 1846). By 1671, quince, apple, pear, cherry, damson [*Prunus domestica* var. *insititia* (L.) Fiori & Paoletti], plum, and common barberry were all commonly grown (Josselyn, 1672). Several of these species [*Prunus avium* (L.) L., *Malus pumila* Mill.] have become naturalized but appear innocuous. However, common barberry's introduction was soon to plague the colonists. *Berberis vulgaris* L. is a host for *Puccinia graminis* f. sp. *tritici*, the stem rust of wheat, and it would be almost three centuries before common barberry was controlled effectively in the United States (Anon., 1937).

Ornamentals, i.e., species introduced purely for aesthetic reasons, were introduced surprisingly early, given the colonists' need to first establish reliable sources of food, fiber, forage, and medicine. By 1672 Josselyn was commenting on the imported ornamentals (lavender cotton, hollyhocks, satin, gillyflowers, pinks, English roses, and eglantine) that he encountered in New England. Eglantine (*Rosa eglanteria* L.) is now naturalized in the United States (Fernald, 1950). Given its early introduction, it may be one of the first European ornamental species to become naturalized in the United States. In introducing ornamentals, the colonists were greatly expanding the taxonomic breadth and geographic range from which naturalized species would be drawn. We lack adequate records of the market in ornamental species that emerged in the 18th century. However, Cutler (1785) reported matter-of-factly that seeds of an *Antirrhinum* species were imported by seed-sellers in New England, and a broadside of "Garden and Grass Seeds, with a choice collection of Flower Roots, & Seeds, Just Imported" was produced as early as 1793 in Richmond, Virginia (National Agricultural Library archives, as cited in Pennsylvania Horticultural Society, 1976).

With the apparent proliferation of seed catalogs by 1800, scores of species were arriving in the United States from a worldwide list of native ranges. Ornamental species (and earliest date of their appearance in a seed catalog published in the United States) include *Lonicera japonica* Thunb. (1823), *Lantana camara* L. (1804), *Melia azedarach* L. (1807), *Mesembryanthemum crystallinum* L. (1807), *Mimosa pudica* L. (1804), *Myrica faya* Dryand (1823), *Rhamnus cathartica* L. (1807), *Rosa multiflora* Thunb. (1826), *Schinus terebinthifolius* Raddi (1832), and *Ulex europaeus* L. (1807) (Mack, 1991). By 1804 a Philadelphia seed merchant could describe himself as someone who had for sale, ". . . an extensive variety of Asiatic, South-Sea Islands, African, and European Seeds, of the most curious and rare kinds; and is daily adding to his collection, as he avails himself of every opportunity to procure seeds from all parts of America, as well as from every part of the world, to which the enterprise of American commerce extends . . ." (B. M'Mahon [1804: 1] "A catalogue of American Seeds . . ."; archives of the National Agricultural Library, Beltsville, Maryland). The speed with which regions only recently colonized by Europeans were contributing species to this global traffic in ornamental plants is impressive. D. & C. Landreth, seed merchants in Philadelphia, offered nine *Melaleuca* species from "New Holland" (Australia) in their 1832 catalog (archives of the Pennsylvania Horticultural Society, Philadelphia). In all likelihood, these species had been imported even earlier

Table 2. Naturalized species in the United States considered by de Schweinitz (1832) to have been deliberately introduced. Some of the names employed by de Schweinitz are not in current nomenclatural usage, and he did not include scientific authorities for the species he listed. His names for these species appear parenthetically. The International Plant Names Index (http://www.ipni.org) was employed as the nomenclatural standard for plant names and authorities.

Agrostis gigantea Roth. (*Agrostis alba*)	*Plantago major* L. (*Plantago major*)
Agrostis tenuis Sibth. (*Agrostis vulgaris*)	*Poa pratensis* L. (*Poa pratensis*)
Anthoxanthum odoratum L. (*Anthoxanthum odoratum*)	*Rosa eglanteria* L. (*Rosa rubiginosa*)
Barbarea vulgaris Ait. f. (*Barbarea vulgaris*)	*Rumex crispus* L. (*Rumex crispus*)
Brassica nigra (L.) W. D. Jakoch (*Sinapis nigra*)	*Rumex obtusifolia* L. [*Rumex. obtusifolius* (sic)]
Cannabis sativa L. (*Cannabis sativa*)	*Salix alba* L. (*Salix alba*)
Chelidonium majus L. (*Chelidonium majus*)	*Salix vitellina* L. (*Salix vitellina*)
Cynoglossum officinale L. (*Cynoglossum officinale*)	*Scleranthus annuus* L. (*Scleranthus annuus*)
Daucus carota L. (*Daucus carota*)	*Stellaria media* L. (*Stellaria media*)
Datura stramonium L. (*Datura stramonium*)	*Taraxacum officinale* Weber (*Leontodon taraxacum*)
Holcus lanatus L. (*Holcus lanatus*)	*Trifolium pratense* L. (*Trifolium pratense*)
Leonurus cardiaca L. (*Leonurus cardiaca*)	*Trifolium repens* L. (*Trifolium repens*)
Marrubium vulgare L. (*Marrubium vulgare*)	*Verbascum blattaria* L. (*Verbascum blattaria*)
Nepeta cataria L. (*Nepeta cataria*)	*Verbascum thapsus* L. (*Verbascum thapsus*)
Pastinaca sativa L. (*Pastinaca sativa*)	*Veronica officinalis* L. (*Veronica officinalis*)
Phleum pratense L. (*Phleum pratense*)	

to Britain before being introduced in the United States.

The flurry of published floras that appeared after 1800 provides some of the best evidence we have of which deliberately introduced species were becoming naturalized. *Salix viminalis* L. ("*Salix viminalis*") (Pursh, 1814), *Crataegus monogyna* Jacq. ("*C. oxyacantha* L.") (Barton, 1818), *Acer negundo* L., *Salix babylonica* L., and *Salix alba* L. (Darlington, 1826) were all recognized as new members of the eastern U.S. flora. Sometimes the flora's author even knew the circumstances of a species' introduction. Darlington (1826) wryly attributed the establishment around West Chester, Pennsylvania, of *Leonurus marrubiastrum* L. to the gardening of Humphrey Marshall, a local horticultural enthusiast (Wilbert, 1908).

De Schweinitz (1832) assembled comprehensive information about deliberately introduced species that were becoming naturalized in the United States. His observations (de Schweinitz, 1832: 148) based on major categories of introduction are particularly informative: species "purposely brought hither to be cultivated, for the purposes of agriculture, or for some real or fancied value they possess" and others that had "been evidently involuntarily introduced with the imported seeds of agricultural plants. . . ." All 31 species that he listed as deliberate introductions (Table 2) remain naturalized in the United States, and a few have become invasive (e.g., *Poa pratensis* L., *Rumex crispus* L., *Verbascum thapsus* L.). Apparently, most of the current worst invaders in the United States had yet to arrive or were still undetected [e.g., *Bromus tectorum* L., *Lonicera japonica* Thunb., *Polygonum cuspidatum* Sieb. & Zucc., *Sorghum halepense* (L.) Pers.].

SEED CONTAMINANTS: EARLY IMMIGRANTS

In an era before herbicides and diligent seed sieving and inspection, seed lots of crop species varied radically in the extent to which they were contaminated with the seeds of extraneous and unwanted species. Some of the earliest records of non-indigenous plants in North America include species that likely arrived from Europe as seed contaminants, e.g., *Rumex acetosella* L. and *Rumex acetosa* L. (Cronon, 1983, and references therein). Many of these species have been intimately associated with crops through the strong selection provided by cultivation and post-harvest storage. Probably all seed-sown crops have their own array of seed mimics (Barrett, 1983); each mimic's phenology from germination to seed maturation is under selection by the cultivation cycle for its associated crop. Through this close synchrony between the life cycle of the crop and its mimics, cultivation applied to the crop could simultaneously benefit the mimics, leading to their naturalization (Mack, 2000).

We have only a sketchy list of species reputedly introduced as seed contaminants in the early settlement of the United States (Table 3). Given the general neglect of seed cleaning, there were, however, many possible immigrants among the ruderals and crop weeds of Europe. The native forage grasses in New England were deemed so unsuitable as forage that by the 1640s a market in European grass seed had already emerged around Narragan-

Table 3. Non-indigenous species in the United States considered by de Schweinitz (1832) to have arrived as seed contaminants among agricultural seeds. Some of the names employed by de Schweinitz are not in current nomenclatural usage, and he did not include scientific authorities for the species he listed. His names for these species appear parenthetically. The International Plant Names Index (http://www.ipni.org) was employed as the nomenclatural standard for plant names and authorities.

Achillea millefolium L. (*Achillea millefolium*)	*Hypericum perforatum* L. (*Hypericum perforatum*)
Agrostemma githago L. (*Agrostemma githago*)	*Lamium amplexicaule* L. (*Lamium amplexicaule*)
Allium vineale L. (*Allium vineale*)	*Leucanthemum vulgare* Lam. (*Chrysanthemum leucanthemum*)
Anthemis cotula L. (*Anthemis cotula*)	*Linaria vulgaris* L. (*Antirrhinum linaria*)
Arctium lappa L. (*Arctium lappa*)	*Lithospermum arvense* L. (*Lithospermum arvense*)
Bromus secalinus L. (*Bromus secalinus*)	*Lolium perenne* L. (*Lolium perenne*)
Capsella bursa-pastoris (L.) Medik. (*Thlaspi bursa pastoris*)	*Plantago lanceolata* L. (*Plantago lanceolata*)
Cerastium fontanum Baumg. (*Cerastium vulgatum*)	*Poa annua* L. (*Poa annua*)
Cerastium glomeratum Thuill. (*Cerastium viscosum*)	*Polygonum aviculare* L. (*Polygonum aviculare*)
Cerastium semidecandrum L. (*Cerastium semidecandrum*)	*Raphanus raphanistrum* L. (*Raphanus raphanistrum*)
Chenopodium album L. (*Chenopodium album*)	*Setaria glauca* (L.) Beauv. (*Setaria glauca*)
Cirsium arevnse (L.) Scop. (*Carduus arvensis*)	*Sisymbrium officinale* (L.) Scop. (*Erysimum officinale*)
Cirsium vulgare (Savi) Ten. (*Cnicus lanceolatus*)	*Sonchus oleraceus* L. (*Sonchus oleraceus*)
*Commelina sativa**	*Urtica dioica* L. (*Urtica dioica*)
Elytrigia repens var. *repens* (L.) Desv. (*Triticum repens*)	*Urtica urens* L. (*Urtica urens*)
	Veronica agrestris L. (*Veronica agrestris*)
	Veronica arvensis L. (*Veronica arvensis*)

* Probably a corruption of *Camelina sativa* L. (Crantz.) (false flax).

sett Bay (Cronon, 1983, and references therein), providing ample opportunity for the importation of seed contaminants. Furthermore, Josselyn's (1672: 216) list, "Of such Plants as have sprung up since the English planted and kept Cattle in New England," includes non-indigenous species that are unlikely to have been introduced deliberately as pasture species but are often found as seed contaminants: "Shepard's purse" [*Capsella bursa-pastoris* (L.) Medik.], "Groundsel" [*Senecio vulgaris* L.], "Sow-thistle" [*Sonchus* sp.], "Cheek-weed" [*Stellaria media* (L.) Vill.]. Cronon (1983: 143) provided an account from 1652 in which settlers in the New Haven (Connecticut) colony were already debating without avail as to whether the ". . . spreading of sorrill [probably *Rumex crispus* L. or *Rumex acetosella* L.] in the corne fields . . ." could be stemmed. Kalm (1770) commented on European introductions that he saw along the North American eastern seaboard in 1748. Kalm (1770: 118) reported the informed opinion of John Bartram and other American botanists that "*Chenopodium album* [*Chenopodium album* L.] . . . is not a native of America, but has been brought over amongst other seeds from Europe." Kalm (1770: 119) also claimed that *Tanacetum vulgare* L., "which grows here and there in the hedges, on the roads, and near houses, was produced from European seeds." It likely arrived both through deliberate introduction (Mack, 1991) and as a seed contaminant.

Some early 19th century local and regional United States floras also cited species that reputedly arrived as seed contaminants. These statements reflect informed opinion, rather than documented cases. Nevertheless, they are among the very few accounts of these species in the United States that are nearly contemporaneous with their arrival. Barton (1818) described the flora in and around Philadelphia. He listed both *Lithospermum arvense* L. and *Lithospermum latifolium* Michx. as "introduced among grass seeds from Europe, but now naturalised." Pursh (1814) attempted to assemble a flora of the United States, although most of his own collections and exchanges originated in the eastern states from Virginia northward. He reported that *Anthoxanthum odoratum* L. ("*Anthoxanthum odoratum*"), *Festuca pratensis* Huds. ("*Festuca elatior*"), and *Centaurea cyanus* L. ("*Centaurea cyanus*") were either ". . . introduced with grass seeds from Europe" (Pursh, 1814: 65, 83) or "brought from Europe with the grain" (Pursh, 1814: 576).

De Schweinitz (1832: 151) provided the first specific attention to non-indigenous species arriving in the United States as seed contaminants. Although he did not provide explicit information as to how he determined which species were "introduced fortuitously with agricultural seeds," his list is nonetheless illuminating (Table 3). These species include many that remain today as crop seed contaminants or are ruderals, or both. All are now naturalized in the United States (Fernald, 1950). Some in his list also arrived through deliberate introduction, e.g., *Hypericum perforatum* L. (Haughton, 1978) and *Urtica dioica* L. (Uphof, 1968).

SEED CONTAMINANTS: A LONG-TERM MODE OF IMMIGRATION

The opportunity for non-indigenous species to arrive in the United States as seed contaminants grew throughout the 19th century, in part, because the United States remained surprisingly dependent on the routine importation of many crop seeds. Hicks (1895: 391) maintained that for an extraordinary list of crop and forage species, including, "alfalfa, beet, borage, broccoli, Brussels sprouts, cauliflower, chicory, cress, endive, kohl-rabi, radish, salsify, spinach, turnip, the seeds are grown abroad, as are also the seeds of many of our grasses, such as crested dog's tail, sheep fescue, meadow foxtail, perennial rye grass, and sweet vernal grass." In addition, "Of the following vegetables about one-half of the seeds are imported: Carrot, eggplant, leek, onion, parsley, parsnip, and pepper." Large fractions of the seeds needed for domestic production of cabbage, celery, chervil, kale, and lettuce were also imported (Hicks, 1895: 391).

Hicks (1895) and others (e.g., Ledoux, 1880; Ball, 1898) realized that such massive seed importation had created enormous opportunities for the inadvertent introduction of unwanted non-indigenous species. Furthermore, they recognized that a cultivated field, carefully tilled to enhance the crop, was equally advantageous for the emergence of extraneous species (Ledoux, 1880). Their concern had been heightened by recent events. An aggressive invader, *Salsola kali* L., had arrived in the 1880s as a contaminant in flax seed from Russia. By 1894 it had already invaded more than 90,000 km^2 in the wheat-producing regions in the Dakotas (Dewey, 1894). McCarthy (1888) contended that most of the weed flora in the United States was originally introduced and disseminated in the packages of imported seeds, an unsubstantiated claim but with some element of justification.

The problem was not, unfortunately, limited to inadequate seed-cleaning. Foreign seed merchants deliberately adulterated crop seeds with commercially worthless species: "charlock" (*Sinapis arvensis* L.) mixed with turnip and rutabaga seeds, "black medic" (*Medicago lupulina* L.) mixed with red clover, English rye mixed with the more valuable tall fescue and Italian rye (Hicks, 1895: 391). Ledoux (1880) reported that the seeds of ruderal species were routinely gathered in Austria and Bavaria for use as seed adulterants. In one 24.5 g sample of *Phleum pratense* L., Nobbe (1871) found 3329 extraneous seeds representing 31 taxa, including *Rumex acetosella* L., *Prunella vulgaris* L., *Cirsium arvense* (L.) Scop., *Sonchus asper* (L.) Hill ("*Sonchus asper* Villars"), and *Spergula arvense* L. In one extreme case, 90 percent of a Canadian seed lot sold in Michigan as clover consisted of extraneous and non-indigenous seeds. The unwanted seeds averaged 132,000 per kilo in this contaminated lot (Hicks, 1895: 393)—a large founder population that could readily benefit from any cultivation upon sowing. Some seed merchants in the United States were aware of this imported hazard. The Philadelphia seed firm I.V. Faust assured customers in its 1888 catalog that "We are most particular in the purchase of our grass seeds to procure them from a source where there is no danger of foreign seeds having become mixed with them, as we fully appreciate the great damage which some of these will create if once introduced upon the soil."

The response to foreign and domestic contamination was a flurry of state and federal legislation to examine commercial seeds, including seeds that had been directly imported from Europe (McCarthy, 1888; Hicks, 1895). Chester (1889) examined seed lots from domestic and foreign sources. Although it is difficult to distinguish between results for domestic and imported seed lots in his data, the litany of non-indigenous species he detected is consistent among all samples; naturalized species typically found in arable land and roadsides were being repeatedly introduced (Table 4). The diligence of the state-appointed seed analysts at the turn of the century led undoubtedly to curbing the introduction of unwanted non-indigenous species in the United States (Brown, 1941). Unfortunately, these regulatory practices were enacted long after many non-indigenous species had repeatedly entered the United States and become naturalized.

Despite the ample opportunity for non-indigenous species to arrive as seed contaminants before 1900, we detected few species for which there is a historic reference to their arrival in that mode; e.g., only 14 species within the central northeastern United States flora. This mode of introduction has nevertheless been significant. Some species not reported by any pre-1900 observer likely arrived in this manner and were simply overlooked. The United States probably derived many of the weeds of European arable fields simply through the frequency of their importation as seed contaminants. Furthermore, many species, such as *Amaranthus hybridus* L., *Anthemis cotula* L., *Capsella bursa-pastoris* (L.) Medik., *Chenopodium album*, *Nepeta cataria*, *Plantago major* L., and *Rumex acetosella* were continually being introduced and dispersed through the eastern United States by seed merchants (Table 4). Although these species had ar-

Table 4. Non-indigenous species detected repeatedly as seed contaminants in domestic and imported crop seeds in the late 19th century (Chester, 1889). Some of the names employed by Chester are not in current nonmenclatural usage, and he did not include scientific authorities for the species he listed. His names for these species appear parenthetically. The International Plant Names Index (http://www.ipni.org) was employed as the nomenclatural standard for plant names and authorities.

Agrostemma githago L. (*Agrostemma githago*)	*Nepeta cataria* L. (*Nepeta cataria*)
Amaranthus hybridus L. (*Amaranthus hybridus*)	*Plantago lanceolata* L. (*Plantago lanceolata*)
Anthemis arvensis L. (*Anthemis arvensis*)	*Plantago major* L. (*Plantago major*)
Capsella bursa-pastoris (L.) Medik. (*Capsella bursa-pastoris*)	*Polygonum* sp.
Carduus arvensis (L.) Scop. (*Cnicus arvensis*)	*Ranunculus* sp.
Chenopodium album L. (*Chenopodium album*)	*Rumex acetosella*
Echium vulgare L. (*Echium vulgare*)	*Rumex crispus* L. (*Rumex crispus*)
Hypericum perforatum L. (*Hypericum perforatum*)	*Setaria* sp.
Leucanthemum vulgare Lam. (*Chrysanthemum leucanthemum*)	*Stellaria media* L. (*Stellaria media*)
Lithospermum arvense L. (*Lithospermum arvense*)	*Verbascum thapsus* L. (*Verbascum thapsus*)

rived before 1800, the potential for an increase in their genetic variation in the United States would have continued long after these species' initial introduction, a function of the different European locales from which later-arriving populations were drawn (Novak & Mack, 2001).

SPECIES WITH UNKNOWN MODE OF IMMIGRATION TO THE UNITED STATES

We were unable to identify a pre-1900 use or other mode of introduction for approximately 30 percent of the species now naturalized in the regions we examined. Any assessment of the modes of introduction in naturalized floras is handicapped by the paucity and reliability of historic records. We avoided relying on common names to trace mode of introduction, unless a species' common name has been used consistently for several hundred years: e.g., henbane (*Hyoscyamus niger* L.), foxglove (*Digitalis purpurea* L.), shepherd's purse (*Capsella bursa-pastoris*). This criterion limited our ability to trace introductions before ca. 1780. Nevertheless, keen observers such as Josselyn (1672) and Kalm (1770) made invaluable observations.

Additional underestimate of deliberate introductions was likely because some species were introduced for unrecorded purposes. Their naturalized descendants are, however, a living link to a pre-1900 agrarian-based economy in the United States that relied on few imported commodities. Solutions to almost all material needs and desires were literally "home grown." Thus, *Hypericum perforatum* was used for medicinal purposes (Darlington, 1859) and as an object in religious services in 18th century Pennsylvania (Haughton, 1978). The dried heads of *Dipsacus fullonum* L. were used to comb wool (Fernald, 1950). If a plant was deemed valuable, its germplasm was imported, even if the likelihood of successful cultivation anywhere in the United States was low (Grieve, 1959; Stillé & Maisch, 1880). We may never discover all the purposes that our resourceful ancestors had for the range of species they so methodically imported.

Species introduced by all accidental (but undetected) modes occur in the Unknown Category, including those that can survive attached or within a vast array of cargo: hay, ballast, packing material, attached to livestock and clothing (Ridley, 1930; Mack, in press). But collectively they appear far less important than deliberate introduction as the mode by which plants have arrived in new ranges in the United States in the last 400 years (Mack, in press).

POST-1900 IMMIGRATION AND NATURALIZATION

Our emphasis has been on the link between pre-1900 plant introduction and subsequent cultivation and naturalization. Plant importation has continued, however, and new species continually become naturalized. Rejmanek and Randall (1994) reported that nine species had become naturalized in California between 1968 and 1993; deliberately introduced species are prominent in this list (*Catalpa bignonioides* Walt., *Nerium oleander* L., *Pinus pinea* L., *Pinus halepensis* Mill.). The post-1900 growth of the naturalized flora in the United States has likely been substantial. Henry and Scott (1981: 318) tallied the dates of introduction for the "alien component of the spontaneous Illinois vascular flora," species that apparently include all naturalized but also adventive species as well. They concluded that the woody and herbaceous component of this non-indigenous flora before 1922 was composed of 440 species; 163 species were added between 1922 and 1955, and another 208 non-indigenous species were added from 1956 to 1978. Many of these post-

Table 5. Tallies for the likely mode of entry (deliberate, accidental, deliberate & accidental, and unknown) for the naturalized angiosperm floras of South Australia, Hawaii, and Northern Europe. Numbers in each column except the last are percentages of the total naturalized flora surveyed. Sources for the modes of introduction are listed in the footnotes.

	Deliberate	Accidental	Deliberate & accidental	Unknown mode of introduction	Number of taxa
South Australia[1]	57	24	0	19	904
Hawaii[2]	57	39	0	4	813
Nordic continental countries[3, A]	36	44	13	<8	559
North Atlantic Islands[3, B]	16	61	9	14	46

[1] Kloot (1987).
[2] Wester (1992).
[3] Weidema (2000).
[A] Numbers are means of percentages for Norway, Sweden, Finland, and Denmark as derived from the data of Weidema (2000).
[B] Numbers are means of percentages for Greenland, Iceland, the Åland Islands, and the Faeroe Islands as derived from the data of Weidema (2000).

1900 plant immigrants to Illinois would have been deliberately introduced, including most, if not all, the woody immigrants (Reichard & Hamilton, 1997).

The proportions among deliberately and accidentally introduced 20th century immigrants that have become naturalized are better documented in Australia. Of the 290 weed, i.e., deleterious plant, incursions into Australia from 1971 to 1995 that have led to naturalizations, 65 percent of these species were introduced as ornamentals, and an additional 7 percent arrived as intended additions to agriculture (Groves, 1998). Thus, more than two-thirds of these species have had some degree of post-immigration cultivation. The proportion of species arriving in Australia through deliberate action continues a pattern set into motion centuries earlier among European colonies and their trading partners.

Detailed examination of the fate of introduced woody ornamental species across much of the 20th century in Canberra, Australia (Mulvaney, 2001), suggests an additional aspect of the importance of post-introduction cultivation. Mulvaney (2001) contended that the probability of a species becoming naturalized is a direct function of the number of recorded plantings of the species from 1909 through the mid 1980s. A similar explanation has been proposed to account for the naturalization of non-indigenous birds in New Zealand; persistence correlates with the intensity of the introduction efforts (Veltman et al., 1996). The more separate opportunities for non-indigenous species to be cultivated, the greater the probability some of its immigrants will be initially spared the full force of environmental stochasticity in the new range.

NATURALIZED SPECIES ARISE FROM DELIBERATE INTRODUCTIONS: A RECURRING PHENOMENON WORLDWIDE

Our chief goal was to evaluate in an objective manner the hypothesis that much of the U.S. naturalized flora has a historic link in its mode of entry to deliberate introduction and post-immigration cultivation. At the outset, we decided that our benchmark for rejecting this hypothesis would be the failure to detect that even half of the naturalized species had a history of pre-1900 use. Our hypothesis appears supported by our tallies (Table 1).

The plausibility of this link is further supported by evidence gathered among naturalized angiosperm floras worldwide. Wester (1992) examined the modes of introduction within the Hawaiian naturalized flora (Table 5). He concluded that the major mode of introduction had been deliberate (57%), and that a large fraction of these species had been introduced in ornamental horticulture. By coincidence, Kloot (1987) also found that at least 57 percent of the South Australia naturalized flora owed its arrival to deliberate transport (Table 5). Esler (1987) determined the modes of introduction (imported for use in either horticulture [including timber and shelter tree species] or agriculture [crop, pasture, and land reclamation], or accidental) for the 303 angiosperm species now naturalized in urban Auckland, New Zealand. Almost 93 percent of this naturalized flora was introduced deliberately, although the degree of post-immigration cultivation probably varies.

Recently, the mode of introduction has been assessed for non-indigenous species in Denmark, Finland, Iceland, Norway, and Sweden along with

the Åland Islands, the Faeroe Islands, and Greenland (Weidema, 2000). Here again, many naturalized species appear to have a history of deliberate introduction (e.g., *Inula helenium* L., *Lychnis chalcedonica* L., *Ornithogalum nutans* L., *Syringa vulgaris* L., *Spiraea salicifolia* L.), but the role of accidental introduction appears to be much larger than in the United States or South Australia. Among Nordic countries in continental Europe, about one-third of the naturalized species are considered to have been deliberately introduced, but more (44%) on average are believed to have been introduced accidentally as seed contaminants of cargo or carried by domesticated animals (Table 5).

These values from northern Europe require further interpretation. Among Nordic investigators there is apparently neither a consensus on the definition of "naturalized" (the values reported may also include adventive species for the floras of some countries) nor on an arrival date before which an immigrant species is deemed native (Weidema, 2000). Potentially more important is the much longer history of agriculture in northern Europe than farming by European colonists in the United States or South Australia. Several millennia of raising crops in northern Europe has given ample opportunity for species to have been introduced, both deliberately and inadvertently (Iversen, 1973). For some of these species, their mode of introduction is unknown [e.g., *Helleborus foetidus* L., *Potentilla micrantha* Ramond ex DC., *Digitalis lutea* L., *Silene tartarica* Pers.] (Weidema, 2000). Furthermore, some fraction of those species now considered native arrived so long ago with human settlement that any identification of erstwhile deliberate use is problematical. The much shorter histories of plant introductions into the "New Europes" in North America, Australia, and South America provide us with a sharper picture of the causes of plant naturalization than can be reconstructed from the records of plant dispersal by humans in Europe.

Needed now is experimentation that bridges the gap between two growing bodies of information: knowledge of the modes of plant introductions and naturalizations since A.D. 1500 (Kloot, 1987; Reichard & Hamilton, 1997; Groves, 1998; Mulvaney, 2001) and understanding of the stochastic forces to which immigrant populations are usually vulnerable (Menges, 1992, 1998; Mack, 1995, 2000). The design of experiments on the fate of immigrant populations (Panetta & Randall, 1994) could benefit from clues derived from the history of plant introductions. Experimental variables, including the sizes of the immigrant populations, the initial entry locales in the new range, and the character and extent of cultivation, could duplicate what is known about a species' early history in its new range. Once such investigations become widespread, our understanding of the causes of plant naturalization and subsequent invasion will likely become much clearer (Williamson, 1999; Williamson & Fitter, 1996).

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Appendix I

Pre-1900 use of some of the naturalized angiosperm species that formed the tallies in Table 1 was indicated by their sale in these 19th century seed catalogs (Archives of the National Agricultural Library, Beltsville, Maryland).

Allen's annual catalogue of seeds. 1870. New York, New York.

Azell Bowditch. 1854. A descriptive catalogue of flower seeds for sale. Boston, Massachusetts.

Barr, G. H. and Co. 1853. Catalogue of agricultural and horticultural implements field and garden seeds and fertilizers.

J. Bartram and Son. 1807. A catalogue of trees, shrubs, and herbaceous plants, indigenous to the United States of America. Philadelphia, Pennsylvania.

B. K. Bliss and Sons. 1870. Catalogue of seeds. Springfield, Massachusetts.

Charles H. B. Breck. 1842. Catalogue of vegetable, herb, tree, flower, and grass seeds, for sale at the New Seed store. Boston, Massachusetts.

Robert Carr. 1828. Bartram's catalogue of trees, shrubs, and herbaceous plants, indigenous to the United States of America. Philadelphia, Pennsylvania.

Bernard M'Mahon. 1804. A catalogue of American seeds, & c. Philadelphia, Pennsylvania.

Bernard M'Mahon. s. d. A catalogue of garden, herbs, flowers, tree, shrub and grass seeds. Philadelphia, Pennsylvania.

Pomeroy and Marshall. 1857. (no title). Mobile, Alabama.

Warren's Garden and Nurseries. 1845. Annual descriptive catalogue of fruit and ornamental trees. Boston, Massachusetts.

Messrs. Winship. 1833. Annual catalog of the fruit and ornamental trees and plants, cultivated for sale at the Brighton Nurseries by Messrs. Winship. Boston, Massachusetts.

Winter and Co. 1841. Catalogue of fruit and ornamental trees. [Linnean Botanic Garden and nursery (late of the messrs. Princes).] Flushing, New York.

Winter and Co. 1844–1845. Catalogue of fruit and ornamental trees. [Linnean Botanic Garden and nursery (late of the messrs. Princes).] Flushing, New York.